Mamm Res (2016) 61:179–186
DOI 10.1007/s13364-016-0270-4

ORIGINAL PAPER

Pattern of parasite egg shedding by European bison (*Bison bonasus*) in the Białowieża Primeval Forest, Poland

Marta Kołodziej-Sobocińska[1] · **Anna M. Pyziel**[2] · **Aleksander W. Demiaszkiewicz**[2] · **Tomasz Borowik**[1] · **Rafał Kowalczyk**[1]

Received: 13 August 2015 / Accepted: 29 March 2016 / Published online: 8 April 2016

Abstract We investigated the pattern of parasite egg shedding by European bison (*Bison bonasus*) in the Białowieża Primeval Forest. We found several groups of parasite eggs in bison faeces including Trichostrongylidae, *Nematodirus* spp., *Aonchotheca* sp., *Trichuris* sp. and *Moniezia* spp. Trichostrongylidae eggs were expelled from bison at the highest percentage (27.8 %) but in low numbers. The prevalence (percentage of faeces with parasite eggs) of other parasites did not exceed 12 %. The number of detected eggs of the parasite species differed: The highest was in *Trichuris* sp. and *Moniezia* spp. There were no significant differences in prevalence between male and female bison, with exception of *Trichuris* sp. whose eggs were more often detected in female faeces. The number of eggs per gram (EPG) of faeces was significantly higher in females for *Aonchotheca* sp. Parasite prevalence showed seasonal variation and was significantly higher for Trichostrongylidae, *Nematodirus* spp., *Aonchotheca* sp. and *Moniezia* spp. parasites in winter (December–March) compared to the snow-free period (April–November). We observed a 3–14 fold higher prevalence of these parasites in winter compared with the snow-free period. We assumed that factors such as season and bison sex have an influence on the level of excreted eggs. The determination of the factors affecting the rate of parasite egg excretion into the environment is important for the management of wild animals, especially endangered species such as the European bison.

Keywords Gastrointestinal parasites · Seasonal pattern · Supplementary feeding · Endangered species · Management practices

Communicated by: Marietjie Landman

✉ Marta Kołodziej-Sobocińska
mksobocinska@ibs.bialowieza.pl

[1] Mammal Research Institute, Polish Academy of Sciences, Waszkiewicza 1, 17-230 Białowieża, Poland

[2] W. Stefański Institute of Parasitology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland

Introduction

Parasites may have significant influence on individuals and populations by changing the behaviour of individual hosts (Lefèvre et al. 2009), regulating host population sizes through direct effects on birth rate and mortality (Møller 2005), mediating competitive interactions among hosts (Thomas et al. 2005) or acting as ecosystem engineers (Thomas et al. 1999).

Studies done world-wide have shown that variations in gastrointestinal parasitic infections are mainly connected with rainfall fluctuations (Chattopadhyay and Bandyopadhyay 2013; Akturazzaman et al. 2013). Adequate moisture and optimum temperature favour the growth and survival of the infective stages of nematodes, leading to higher contamination of pastures or food (Regassa et al. 2006; Shirale et al. 2008). It has also been shown that seasonal changes in the impact of parasites on hosts may influence immune function, for example, when connected with the breeding season (Møller et al. 2003). In addition, host condition, which is often correlated with host population density, is likely to influence parasite virulence (Donnelly et al. 2012). In more seasonal environments, it has been suggested that if density-dependent virulence is widespread, wildlife disease is likely to be more virulent (Donnelly et al. 2012).

The significant impact of parasites on the population dynamics of wildlife has emerged as a critical issue in the conservation of threatened species. Mounting evidence indicates

that infectious agents can considerably influence local populations by causing temporary or permanent decline of their numbers (Thompson et al. 2010). Therefore, understanding the role of infectious agents in shaping wildlife dynamics requires accurate data on the diversity and abundance of potential pathogens in natural ecosystems, especially at the local scale (Smith et al. 2009).

The European bison (*Bison bonasus* L., 1758) is the largest terrestrial mammal in Europe. After extinction in the wild in 1919, it was restored from captive survivors and reintroduced to over 30 locations in eastern Europe (Pucek et al. 2004). The world population of the species has been increasing (3310 free-living bison in 2013) (Raczyński 2014). However, free-ranging populations are small (only 9 populations have over 100 individuals) and isolated by geographical distance. The bison population in the Białowieża Primeval Forest (BPF) is the largest in the world (965 individuals in total in the Polish and Belarusian parts of the Forest), and it constitutes the core of the global population of the species (29 % of free-ranging bison). Apart from lack of connectivity between isolated populations and their small size, the other threats to bison are low genetic variation due to a severe genetic bottleneck (Tokarska et al. 2011), as well as diseases and parasites (Pucek et al. 2004). Although bison are traditionally managed in forest habitats, increasing evidence shows that bison are a refugee species adapted to open and mixed habitats (Kerley et al. 2012; Bocherens et al. 2015). Most free-ranging populations of bison inhabiting forests are supplied with food in the winter which mitigates migrations and reduces farm crop depredation. This leads to unnatural winter aggregations, strong decline of individual home range size, and an increase of local winter densities of bison (Krasińska et al. 2000; Radwan et al. 2010). Within several years of the restoration, bison assimilated several new species of parasites. This included the blood-sucking nematode of abomasa *Ashworthius sidemi* (Trichostrongylidae) which is specific to Asian deer species (Dróżdż et al. 2000, 2003). The invasion of a new, dangerous parasite in the endangered population of bison in the BPF is alarming in light of the observed decline in their physical condition and the increasingly female-biased calf sex ratio. This is as predicted by Trivers-Willard hypothesis and may be associated with an increase in parasitic load especially the invasive *A. sidemi* (Hayward et al. 2011). In recent years, the presence of *A. sidemi* was confirmed genetically in cattle (Moskwa et al. 2015). This indicates the possible transmission of the parasite from wildlife to livestock.

The European bison population is widespread in the forest and forest surroundings at an area covering around 800 km^2 (Kowalczyk et al. 2013). Males live alone (62 % of males) or in small bull groups, while females with calves and subadults roam in groups numbering on average 11–15 individuals (Krasińska and Krasiński 1995, 2013; Krasińska et al. 2000). Higher aggregations of bison occur during the rutting season (August–October). These behavioural traits are responsible for higher infection rates among females and yearlings. During the winter (December–March), most bison concentrate around feeding sites where they are supplementary fed with differing intensity. They stay in very limited ranges, sometimes for over 4 months, in herds up to 70 individuals (Hofman-Kamińska and Kowalczyk 2012; Kowalczyk et al. 2011). This is the second factor favouring inter-individual transmission of parasites in the bison population.

In this study, we aimed to investigate seasonal pattern and sexual differences in intestinal helminth egg excretion in wild bison. We predicted that both the prevalence and number of eggs per gram (EPG) of faeces would be higher in winter and among females. Our hypotheses were due to both the observed differences in social behaviour of bison cows and bulls and the increased contact rate between individuals at feeding sites in winter.

Material and methods

Study area

The study was conducted in the Polish part (ca. 600 km^2) of the Białowieża Primeval Forest (BPF; 52° 29′–52° 37′ N, 23° 31′–24° 21′ E) located along the Polish-Belarusian border.

The climate of the BPF is transitional between Atlantic and continental types with clearly marked cold and warm seasons. Meteorological data have been collected daily since 2000. The mean annual temperature is +8.0 °C. The mean temperature of the coldest month—January—is −3.5 °C. The warmest month is July with a mean temperature of +19.9 °C. The vegetative season lasts on average 215 days (range 198–238) and was calculated by Tylkowski (2013). Snow cover has persisted from 41 to 120 days per year with a maximum recorded depth of 55 cm. Mean annual precipitation is 650 mm.

Faeces collection and analyses

This study was based on analysis of faecal parasitic load and was conducted during a 12-month period from April 2008 to March 2009 in the Polish part of the Białowieża Primeval Forest. Each month, usually in the morning, fresh faecal samples were collected separately from males and females (12 samples of each sex). Faeces were collected from radio-collared individuals, and herds with collared bison (15 to 25 individuals are tracked annually) or occasionally from non-collared individuals, always after visual sex identification. Our sampling strategy included both temporal and spatial stratification to avoid pseudo replication. Usually, the same herds or individuals were not sampled more than once within 1 month to secure as random sampling as possible. This was possible due to the spatial and social organisation of the bison population (Krasińska and Krasiński 1995; Krasińska et al.

2000) and the distribution of individuals and herds (in total 451–456 bison in 2008–2009) (Raczyński 2009, 2010) across the 800 km^2 area. The samples were put into 30-ml labelled tubes. All samples were stored for up to 1 month at −20 °C and investigated immediately after defrosting. Detected eggs of parasites maintained their morphological figures typical for the genus. Up to date, we have not observed any damages in eggs structure that were previously preserved by freezing the faeces for few weeks (Demiaszkiewicz, pers. commun.). In total, 288 faecal samples were collected (144 for males and 144 for females). The same materials were used to study the annual pattern of shedding *Eimeria* spp. oocysts in European bison (Pyziel et al. 2011).

Three grams of each sample were examined for helminth eggs by direct flotation in saturated sucrose solution (specific gravity 1.27) with the use of a centrifuge (Taylor et al. 2007). Samples were investigated using an Olympus BX50 light microscope at ×100–400 magnification. The eggs were determined to the family or genus according to their dimensions and morphological figures (Shorb 1939; Taylor et al. 2007).

We used two measures to describe parasitic load: (1) the prevalence denoted the percentage of faeces with parasite eggs and (2) EPG—number of eggs per gram of faecal sample. Prevalence in this study do not reflect the proportion of bison infected, but the proportion of bison shedding parasite eggs, and we used this term to avoid longer explanation each time we talk about the proportion of faeces with bison parasites. Parasite egg number in faeces does not directly show infection intensity, which is possible to get by carrying out dissection analysis (Dróżdż et al. 2000). However, in the case of protected and endangered species such as European bison, this is the only method that allows the collection of samples for parasitological studies throughout the year and to track seasonal changes in parasite load. The number of excreted eggs stated in coprological studies can depend on the parasite. This is due to differences in the parasite's biology, life cycle, or prepatent period. Therefore, we have not compared one parasite to another but followed the seasonal changes within each parasite separately.

Statistical analysis

To model which factors affect the prevalence and number of parasite eggs in bison faeces, we described the following set of parameters for all sampled faeces: the presence and the number of parasite eggs (separately for each parasite group), sex of the bison, and the season when samples were collected (winter: December–March; snow-free period: April–November). In order to analyse factors affecting the prevalence of each parasite group, we fitted generalised linear models (GLM) for binomial data (Zuur et al. 2009). We set the probability of the bison to be infected as a dependent binominal variable: "1" was attributed to parasite presence and "0" to parasite absence. Number of eggs per gram of faeces was calculated for the parasites in which the highest numbers of positive samples were found—Trichostrongylidae and *Aonchotheca* sp.—and we fitted negative binomial generalised linear models (negative binomial GLM) for count data which dealt with observed overdispersion of models (Zuur et al. 2009). For each parasite group, we ran separate models with the main effects of the explanatory variables (season and bison sex). Final models comprised only significant factors ($P<0.05$).

We checked the normality and homoscedasticity in the distribution of the final model residuals by inspecting the quantile-quantile distribution plot and model residuals against plots of fitted values (estimated responses). All statistical analyses were completed in R (version 3.1.2; R Development Core Team 2014).

Results

We found eggs of four types of gastrointestinal nematodes from the genus *Aonchotheca*, *Nematodirus*, *Trichuris*, and Trichostrongylidae family and tapeworm eggs from the genus *Moniezia*, in bison faeces in the BPF. Trichostrongylidae eggs were expelled from bison at the highest percentage (27.8 %) but in low numbers (Table 1). The prevalence of other parasites did not exceed 12 %. Parasite species differed in EPGs, which was the highest in *Trichuris* sp. and *Moniezia* spp. (Table 1). For most of the period without snow cover, no eggs of *Aonchotheca* sp., *Nematodirus* spp. and *Moniezia* spp. were found (Figs. 1 and 2). *Trichuris* sp. eggs showed no pattern of seasonality and they were expelled at a regular intervals (Fig. 1).

Binomial generalised linear models (GLMs) were used to describe the effects of season and bison sex on the probability of bison to be infected with Trichostrongylidae (Tricho), *Aonchotheca* sp. (Aonch), *Trichuris* sp. (Trichu), *Nematodirus* spp. (Nemat) and *Moniezia* spp. (Monie) (Table 2). Averaged negative binomial generalised linear models (GLMs) were used to describe the effects of season and bison sex on the EPGs of Trichostrongylidae (Tricho) and *Aonchotheca* sp. (Aonch) infections in bison (Table 3). The models revealed that with the exception of *Trichuris* sp., whose eggs were more often detected in female faeces ($P=0.01$), there were no significant differences in the prevalence of infections between bison males and females (Tables 1 and 2). EPG was significantly higher in females for *Aonchotheca* sp. eggs ($P=0.04$) (Table 3).

The prevalence and the number of eggs excreted by European bison showed seasonal variation (Figs. 1, 2 and 3). A comparison of parasite prevalence between winter (December–March) and the snow-free period (April–November) revealed that in winter, a significantly higher share of individuals were infected (Trichostrongylidae: $P<0.001$, *Aonchotheca* sp.: $P<0.001$, *Moniezia* spp.: $P=0.008$ and

Table 1 The mean number of parasite eggs in one gram of faeces (EPG) and their prevalence values in European bison males ($n = 144$) and females ($n = 144$) in the Białowieża Primeval Forest

	Mean EPG						Prevalence (%)		
Genus	Females	N_p	Males	N_p	All	N_p	Females	Males	All
Trichostrongylidae	3.3 (1–24)	42	3.6 (1–23)	38	3.38 (1–24)	80	29.2	26.4	27.8
Nematodirus spp.	8.7 (1–39)	6	3.3 (1–9)	4	6.5 (1–39)	10	4.2	2.8	3.5
Aonchotheca sp.	6.9 (1–42)	17	3.3 (1–19)	16	5.58 (1–42)	33	11.8	11.1	11.5
Trichuris sp.	100.9 (1–246)	13	25.0 (25)	1	88.4 (1–246)	14	9.0	0.7	4.9
Moniezia spp.	148.3 (2–384)	4	5.0 (1–12)	5	68.7 (1–384)	9	2.8	3.5	3.1

Mean, ranges (in brackets) and number of positive samples (N_p) are given. Significant differences in *Trichuris* sp. prevalence ($P = 0.01$; see Table 2)

Nematodirus spp.: $P = 0.02$) (Table 2, Fig. 2). In winter, the prevalence of these parasites was 3–14 fold higher than observed in the snow-free period. Parasite prevalence showed seasonal variation, with the highest values recorded in the winter months: Trichostrongylidae, March (91.7 %); *Aonchotheca* sp., January (58.3 %); *Moniezia* spp., January (20.8 %); and *Nematodirus* spp., January (12.5 %) (Fig. 1). In addition, in winter, EPG of Trichostrongylidae was higher than in the snow-free period ($P = 0.004$) (Table 3, Fig. 3).

Discussion

The parasitic fauna of European bison has been well described. A total of 88 species of parasites have been discovered in 100 years of investigations (Karbowiak et al. 2014a, b). There is an increasing trend in parasite species richness as well as the prevalence and intensity of infections. This could be caused by possible transmission from other ruminants or the increased contact rate between bison in winter due to their high density arising from supplementary feeding in fixed locations (Karbowiak et al. 2014b; Radwan et al. 2010; Pyziel et al. 2011). It is known that European bison are infested with parasite larvae through contact with contaminated water and pastures (Treboganova 2010). Constant and long-term use of the same area during winter causes an accumulation of invasive material and increased risk of helminth invasions (Treboganova 2010).

In our study, the eggs of four types of gastrointestinal nematodes and one tapeworm were recorded. The prepatent period—the time between the infection of the host and the appearance of the first eggs in faeces—lasts from 2–4 weeks in Trichostrongylidae and *Nematodirus* spp. (Skrjabin et al. 1954) to 7–8 weeks in *Trichuris* sp. (Skrjabin et al. 1957) and 9–12 weeks in *Anchieta* sp. (Moravec et al. 1987). After this time, female nematodes lay eggs which are released into the environment with the host faeces. The development of the third stage invasive larvae takes from 5 to 15 days in Trichostrongylidae, 15 to 30 days in *Nematodirus* spp., 23 to 25 days in *Trichuris* sp. and up to 54 to 62 days in *Aonchotheca* sp. (Skrjabin et al. 1954; 1957; Moravec et al. 1987). The life cycle of *Moniezia* spp. of tapeworms is complex; they utilise *Oribatida* sp. mites as intermediate hosts and have a prepatent period that lasts 5–7 weeks (Połeć and Moskwa 1994). A relatively short prepatent period suggests that the aggregation of bison in winter may cause effective transmission of parasites and increased parasitic load within this period.

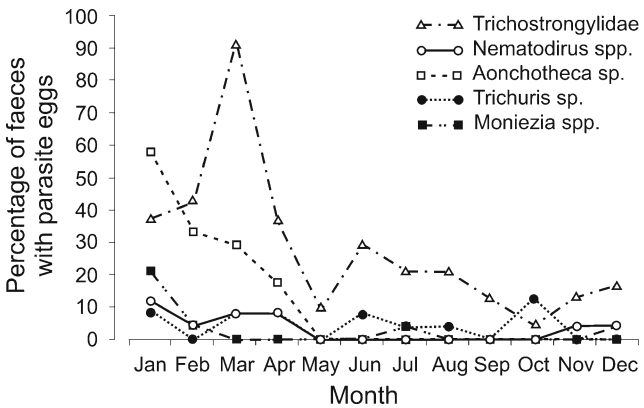

Fig. 1 The annual cycle of parasite egg prevalence in European bison faeces ($n = 288$) in the Białowieża Primeval Forest

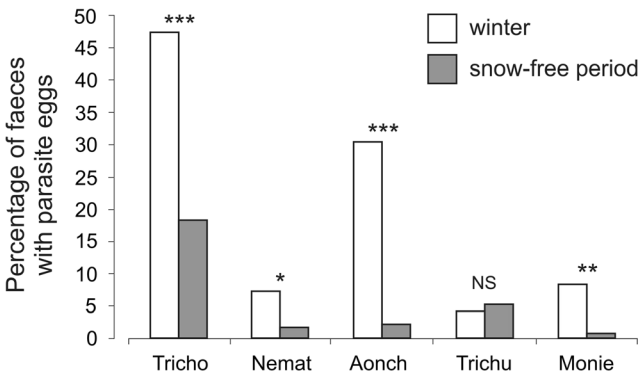

Fig. 2 Percentage of European bison excreting parasite eggs during winter (December–March) and the snow-free period (April–November) in the Białowieża Primeval Forest. Trichostrongylidae (Tricho), *Aonchotheca* sp. (Aonch), *Trichuris* sp. (Trichu), *Nematodirus* spp. (Nemat) and *Moniezia* spp. (Mon). ***$P < 0.001$; **$0.001 < P < 0.01$; *$0.01 < P < 0.05$

Table 2 Parameter estimates for the binomial generalised linear models (GLMs), describing effects of season and bison sex on the probability of bison to be infested with Trichostrongylidae (Tricho), *Aonchotheca* sp. (Aonch), *Trichuris* sp. (Trichu), *Nematodirus* spp. (Nemat) and *Moniezia* spp. (Mon) in the BPF in 2008–2009

Variables	Estimate	SE	*z* value	*P* value
Tricho				
Intercept	−1.42	0.23	−6.23	<0.001
Season winter (snow-free period)	1.37	0.28	4.94	<0.001
Sex male (female)	−0.14	0.28	−0.53	0.60
Aonch				
Intercept	−3.80	0.54	−7.03	<0.001
Season winter (snow-free period)	3.01	0.55	5.45	<0.001
Sex male (female)	−0.08	0.41	−0.20	0.84
Trichu				
Intercept	−2.23	0.34	−6.54	<0.001
Season winter (snow-free period)	−0.24	0.62	−0.40	0.69
Sex male (female)	−2.64	1.04	−2.53	0.01
Mon				
Intercept	−5.37	1.07	−5.00	<0.001
Season winter (snow-free period)	2.85	1.07	2.67	0.008
Sex male (female)	0.24	0.70	0.35	0.73
Nemat				
Intercept	−3.95	0.64	−6.18	<0.001
Season winter (snow-free period)	1.60	0.70	2.28	0.02
Sex male (female)	−0.42	0.66	−0.64	0.52

Season—snow-free period, winter. Sex—female, male. Reference levels for analysed factors are presented in parenthesis

The prevalence and number of eggs described in our study were relatively low, with the exception of eggs of the Trichostrongylidae family. This group includes parasites such as *A. sidemi* or Ostertagiinae, which have previously been reported in large numbers in European bison (Dróżdż et al. 2002, 2003; Demiaszkiewicz and Lachowicz. 2007; Demiaszkiewicz and Pyziel 2010; Demiaszkiewicz et al. 2012). They also have the shortest prepatent period and time required for the development of infective larvae (Skrjabin et al. 1954); this favours the possibility of re-infection. Similar (24.3 %) overall prevalence of *Eimeria* spp. invasion studied on the basis of the same faecal samples was found, but with much higher oocyst count per gram of faeces (OPG) (Pyziel et al. 2011). However, no symptoms of clinical coccidiosis were observed.

Table 3 Parameter estimates for the negative binomial generalised linear models (GLMs), describing the effects of season and bison sex on the number of Trichostrongylidae (Tricho) and *Aonchotheca* sp. (Aonch) eggs per gram of faeces (EPG) in bison population in the BPF in 2008–2009

Variables	Estimate	SE	*z* value	*P* value
Tricho				
Intercept	0.82	0.19	4.24	<0.001
Season winter (snow-free period)	0.61	0.21	2.89	0.004
Sex male (female)	0.005	0.21	0.02	0.98
Aonch				
Intercept	1.79	0.45	3.97	<0.001
Season winter (snow-free period)	0.25	0.51	0.48	0.63
Sex male (female)	−0.72	0.34	−2.10	0.04

Season—snow-free period, winter. Sex—female, male. Reference levels for analysed factors are presented in parenthesis

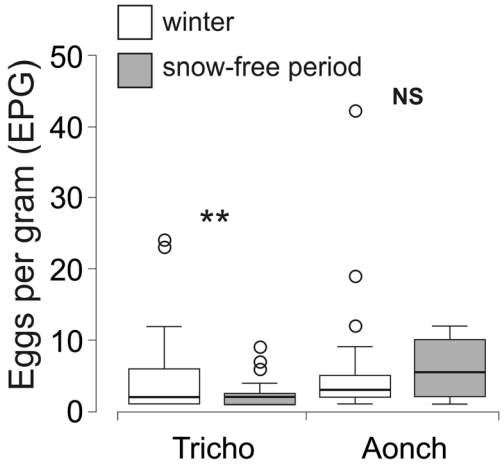

Fig. 3 Number of Trichostrongylidae and *Aonchotheca* sp. eggs per gram of faeces (EPG) during winter (December–March) and the snow-free period (April–November) in the Białowieża Primeval Forest. Trichostrongylidae (*Tricho*) and *Aonchotheca* sp. (*Aonch*). **$0.001 < P < 0.01$

A. sidemi is a pathogenic, blood-sucking nematode of the abomasum which infested Polish populations of European bison in 1999 (Dróżdż et al. 2002). This parasite, which originated from Asian cervids (mainly the sika deer *Cervus nippon*), was dissected from culled bison in the BPF for the first time in 2000 (Demiaszkiewicz et al. 2008). From 2004 to 2011, all the culled bison were found to be infected with this parasite (Demiaszkiewicz et al. 2008; Demiaszkiewicz and Pyziel 2010), but since then, the prevalence of infections has been decreasing (Kołodziej-Sobocińska pers. commun).

No difference in parasitic infection was found between bison sexes, with the exception of *Trichuris* sp. prevalence and number of *Aonchotheca s*p. eggs excreted, which was higher in females. Similar pattern was observed for *Eimeria* spp. Oocysts were more prevalent in bison cows (35 %) than in bison bulls (14 %) (Pyziel et al. 2011). Recent studies have revealed that male-biased parasitism is not universal and that there are many other factors which influence parasite infection such as age of individuals, sexual size dimorphism, level of hormones, individual host's variability (i.e. behavioural, physiological) or immunocompetence (Kiffner et al. 2013). In the BPF, higher parasite infection prevalence and the intensity of some parasites in females may result from (1) the bigger herds formed by cows, leading to a higher rate

of parasite transmission between individuals, compared to males which roam solitarily or in small groups (Radwan et al. 2010; Pyziel et al. 2011); and (2) immunosuppression caused by pregnancy, which may facilitate the observed pattern (Lloyd 1983; Krishnan et al. 1996). According to previous studies, levels of EPGs and OPGs (oocysts per gram) as well as diversity of parasite composition were higher among the youngest cattle and bison living in high densities (ex. captive individuals) (Höglund et al. 2002; Pyziel et al. 2014). A number of factors not tested in the present study could influence the course of parasite invasion (Lloyd 1983; Wakelin 1985; Stear et al. 1999; Bush et al. 2001). In some studied parasites, the relatively low infection prevalence and intensity, based on the detection of eggs in faeces, could be the reason for not finding differences between the sexes.

We found a seasonal pattern of parasite egg shedding by bison in the BPF. In winter, we registered a higher prevalence of excreted eggs from Trichostrongylidae family, *Aonchotheca* sp., *Moniezia* spp. and *Nematodirus* spp. Trichostrongylidae eggs were also more numerous in this period. A similar pattern was observed in elk (*Cervus elaphus*) in Wyoming, USA (Hines et al. 2007). In winter (November–April), supplementary fed elk had significantly more gastrointestinal nematode eggs than non-fed individuals in January and February but, interestingly, significantly less in April. This was explained by improved nutrition on the feed grounds (Hines et al. 2007). To explain the seasonality of infectious diseases, with maximum values during winter, several factors were proposed such as host social behaviour, high contact rates, harsh weather conditions, poorer nutrition and investment in reproduction causing a weakened immune system (London and Yorke 1973; Finkenstädt et al. 1998; Newton-Fisher et al. 2000; Dowell 2001; Hosseini et al. 2004; Altizer et al. 2006). A decline of 10 % in the body condition of bison in winter has been recorded (Hayward et al. 2015). Study by Pyziel et al. (2011) revealed the highest prevalence of *Eimeria* spp. oocysts in bison faeces in early spring and significant influence of winter aggregations of bison on coccidian oocysts shedding.

In addition, some free-living stages of species from Trichostrongylidae family (e.g. *Trichostrongylus colubriformis*, *Teladorsagia circumcincta* in sheep) are known to be resistant to low temperatures; therefore, they may infect hosts during the winter season (O'Connor et al. 2006). For many parasites, transmission depends on host encounters with parasite stages present in the environment (Altizer et al. 2006). It is thought that both eggs and larvae are present in bison faeces year round (Demiaszkiewicz pers. commun.); however, such studies in wild ruminants have not been conducted.

Seasonal aggregation caused by the increased use of water sources, fruiting trees during the dry season, or dens and supplementary feeding sites in winter may have epidemiological consequences for animals (Gremilion-Smith and Woolf 1988; Altizer et al. 2006; Radwan et al. 2010; Navarro-Gonzalez et al. 2013; Kołodziej-Sobocińska et al. 2014). European bison behaviour varies between summer and winter. They spend summer in smaller herds roaming on larger ranges, while in winter, most individuals aggregate around supplementary feeding sites and use limited area (Krasińska and Krasiński 1995; Krasińska et al. 2000; Radwan et al. 2010). Therefore, the high population density at feeding sites in winter may facilitate parasite transmission due to the repeated defecation of bison in fixed locations. The relationship between winter densities of bison at feeding sites and blood-sucking nematode *A. sidemi* prevalence in the BPF was showed by Radwan et al. (2010). Recent data from dissected individuals revealed much higher *A. sidemi* infection intensity for supplementary fed bison, which form large herds (Kołodziej-Sobocińska pers. commun.).

Previous studies proved that the significant reduction of parasite egg shedding in the warm, snow-free period could be caused by several factors including lower bison densities, higher food availability and overall improved condition of the bison, the "self-cure" phenomenon or a stronger immune response (von Szokolay and Rehbinder 1984; Møller et al. 2003; Altizer et al. 2006; Hines et al. 2007). In fallow deer, a "spring-rise" of Trichostrongylidae, *Trichuris* sp. and *Aonchotheca* sp. was observed during the late winter-early spring period following a "self-cure" response (von Szokolay and Rehbinder 1984). Studies of the "self-cure" phenomenon in sheep infected with *Haemonchus contortus*, under field conditions in East Africa, revealed that the onset of "self-cure", as judged by a dramatic fall in faecal egg counts, was found to be simultaneous in sheep grazing on both infected and uninfected pastures (Allonby et al. 1973). Furthermore, the results of autopsies carried out before and after self-cure showed that a remarkable and equal loss of adult worm burdens had also occurred. These results indicate that "self-cure" of *H. contortus* infections under natural conditions occurs in the absence of reinfection and is apparently non-immunological in origin. Since the phenomenon is always associated with a period of significant rainfall, it has been suggested that new growth of pasture may be a significant etiological factor (Allonby et al. 1973). The limited rate of reinfection after bison spread out in spring may explain the pattern observed in the BPF.

It has been established that gastrointestinal nematode invasions are the most widely spread infections among wild ruminants. The health status of the bison population in the BPF has been monitored since its restoration to the wild in the 1950s (Dróżdż 1961). Previous studies were aimed mainly at the monitoring of the prevalence and intensity of parasite infections (Demiaszkiewicz et al. 2012; Karbowiak et al. 2014a, b) but rarely surveyed seasonal and sexual patterns or factors which may have

influenced parasitic invasions (Radwan et al. 2010; Pyziel et al. 2011).

Our study revealed a significantly higher percentage of bison excreted Trichostrongylidae, *Aonchotheca* sp., *Moniezia* spp. and *Nematodirus* spp. eggs in winter and an influence of bison sex on parasite egg shedding in *Trichuris* sp. and *Aonchotheca* sp. This increases our understanding and deepens our knowledge about factors involved in the spread of parasites and their seasonal variation in wild populations of ungulates. This knowledge may benefit the conservation management of endangered species such as the European bison to reduce the impact of different threats and to design proper management activities.

Acknowledgments The study was financed by the Polish Ministry of Science and Higher Education project no. NN304 253435.

We would like to thank Dr. Zbigniew Krasiński and Tomasz Kamiński for help in collecting faecal samples in the field. Mr. Tomasz Diserens for correcting the English.

References

Akturazzaman M, Rony SA, Islam MA, Yasin MG, Rahman AKMA (2013) Concurrent infection and seasonal distribution of gastrointestinal parasites in cross-bred cattle of Sirajganj district in Bangladesh. Vet World 6:720–724. doi:10.14202/vetworld.2013.720-724

Allonby EW, Urquhart GM (1973) Self-cure of *Haemonthus contortus* infections under field conditions. Parasitology 66:43–53

Altizer S, Dobson A, Hudson P, Pascual M, Rohani P (2006) Seasonality and the dynamics of infectious diseases. Ecol Lett 9:467–484

Bocherens H, Hofman-Kamińska E, Drucker DG, Schmölcke U, Kowalczyk R (2015) European bison as a refugee species? Evidence from isotopic data on early holocene bison and other large herbivores in Northern Europe. PLoS ONE 10(2):e0115090

Bush AO, Fernandez JC, Esch GW, Seed JR (2001) Immunological, pathological, and biochemical aspects of parasitism. In: Bush AO, Fernandez JC, Esch GW, Seed JR (eds) Parasitism. The Diversity and Ecology of Animal Parasites. Cambridge Unversity Press, UK, pp 13–42

Chattopadhyay AK, Bandyopadhyay S (2013) Seasonal variations of EPG levels in gastro-intestinal parasitic infection in a southeast Asian controlled locale: a statistical analysis. Springer Plus 2:205. http://www.springerplus.com/content/2/1/205

Demiaszkiewicz AW, Lachowicz J (2007) Wzrost zarażenia żubrów helmintami w Puszczy Białowieskiej. In: Olech W (ed.) Rola hodowli ex situ w procesie restytucji żubra. (Ed.). Lasy Państwowe, Gołuchów, pp 12–16 (In Polish)

Demiaszkiewicz AW, Pyziel AM (2010) Forming of European bison helminth fauna in Białowieża Forest. In: Kowalczyk R, Ławreszuk D, Wójcik JM (eds) European bison conservation in the Białowieża Forest. Threats and prospects of the population development. Zakład Badania Ssaków, Białowieża, pp 63–74

Demiaszkiewicz AW, Pyziel AM, Lachowicz J (2008) Helminthological status of European bison in Białowieża Forest in the winter 2007/2008. Eur Bison Conserv Newsl 1:42–52 (In Polish)

Demiaszkiewicz AW, Pyziel A, Kuligowska I, Lachowicz J, Krzysiak M (2012) Nematodes of the large intestine of the European bison of the Białowieża National Park. Ann Parasitol 58:9–13

Donnelly R, Best A, White A, Boots M (2012) Seasonality selects for more acutely virulent parasites when virulence is density dependent. P Roy Soc B-Biol Sci 280:20122464. doi:10.1098/rspb.2012.2464

Dowell SF (2001) Seasonal variation in host susceptibility and cycles of certain infectious diseases. Emerg Infect Dis 7:369–373

Dróżdż J (1961) A study on helminths and helminthiases in bison, *Bison bonasus* (L.) in Poland. Acta Parasitol 9:55–96

Dróżdż J, Demiaszkiewicz AW, Lachowicz J (2000) Aswortioza – nowa parazytoza dzikich przeżuwaczy. Medycyna Weterynaryjna 56:32–35 (In Polish)

Dróżdż J, Demiaszkiewicz AW, Lachowicz J (2002) Kształtowanie się fauny nicieni żołądkowo-jelitowych wolno żyjących żubrów w Puszczy Białowieskiej w ciągu ostatnich 17 lat (1984–2001). Wiad Parazytol 48:375–381 (In Polish)

Dróżdż J, Demiaszkieiwcz AW, Lachowicz J (2003) Expansion of the Asiatic parasite *Ashworthius sidemi* (Nematoda, Trichostrongylidae) in wild ruminants in Polish territory. Parasitol Res 89:94–97. doi:10.1007/s00436-002-0675-7

Finkenstädt B, Keeling MJ, Grenfell BT (1998) Patterns of density dependence in measles dynamics. P Roy Soc B-Biol Sci 265:753–762

Gremilion-Smith C, Woolf A (1988) Epizootiology of skunk rabies in North America. J Wildl Dis 24:620–626

Hayward MW, Kowalczyk R, Krasiński ZA, Krasińska M, Dackiewicz J, Cornulier T (2011) Restoration and intensive management have no effect on evolutionary strategies. Endanger Species Res 15:53–61

Hayward MW, Ortmann S, Kowalczyk R (2015) Risk perception by endangered European bison *Bison bonasus* is context (condition) dependent. Landscape Ecol. doi:10.1007/s10980-015-0232-2

Hines AM, Enzewa VO, Cross P, Rogerson JD (2007) Effects of supplemental feeding on gastrointestinal parasite infection in elk (*Cervus elaphus*): preliminary observations. Vet Parasitol 148:35–355

Hofman-Kamińska E, Kowalczyk R (2012) Farm crops depredation by European bison (*Bison bonasus*) in the vicinity of forest habitats in northeastern Poland. Environ Manage 50:530–541

Hosseini PR, Dhondt AA, Dobson A (2004) Seasonality and wildlife disease: how seasonal birth, aggregation and variation in immunity affect the dynamics of *Mycoplasma gallisepticum* in house finches. P Roy Soc B-Biol Sci 271:2569–2577

Höglund J, Svensson C, Hessle A (2002) A field survey on the status of internal parasites in calves on organic dairy farms in southwestern Sweden. Vet Parasitol 99:113–128

Karbowiak G, Demiaszkiewicz AW, Pyziel AM, Wita I, Moskwa B, Wereszko J, Bień J, Goździk K, Lachowicz J, Cabaj W (2014a) The parasitic fauna of the European bison (*Bison bonasus*) (Linnaeus, 1758) and their impact on the conservation. Part 1. The summarizing list of parasites noted. Acta Parasitol 59:363–371. doi:10.2478/s11686-014-0252-0

Karbowiak G, Demiaszkiewicz AW, Pyziel AM, Wita I, Moskwa B, Wereszko J, Bień J, Goździk K, Lachowicz J, Cabaj W (2014b) The parasitic fauna of the European bison (*Bison bonasus*) (Linnaeus, 1758) and their impact on the conservation. Part 2. The structure and changes over time. Acta Parasitol 59:372–379. doi:10.2478/s11686-014-0253-z

Kerley GIH, Kowalczyk R, Cromsigt JPGM (2012) Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35:519–529. doi:10.1111/j.1600-0587.2011.07146.x

Kiffner C, Stanko M, Morand S, Khokhlova IS, Shenbrot GI, Laudisoit A, Leirs H, Hawlena H, Krasnov BR (2013) Sex-biased parasitism is not universal: evidence from rodent-flea associations from three biomes. Oecologia 173:1009–1022. doi:10.1007/s00442-013-2664-1

Kołodziej-Sobocińska M, Zalewski A, Kowalczyk R (2014) Sarcoptic mange vulnerability in carnivores of the Białowieża Primeval Forest, Poland: underlying determinant factors. Ecol Res 29:237–244. doi:10.1007/s11284-013-1118-x

Kowalczyk R, Taberlet P, Coissac E, Valentini A, Miquel C, Kamiński T, Wójcik JM (2011) Influence of management practices on large herbivore diet – case of European bison in Białowieża Primeval Forest (Poland). Forest Ecol Manag 261:821–828. doi:10.1016/j.foreco.2010.11.026

Kowalczyk R, Krasińska M, Kamiński T, Górny M, Struś P, Hofman-Kamińska E, Krasiński ZA (2013) Movements of European bison (*Bison bonasus*) beyond the Białowieża Forest (NE Poland): range expansion or partial migrations? Acta Theriol 58:391–401. doi:10.1007/s13364-013-0136-y

Krasińska M, Krasiński Z (1995) Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest. Acta Theriol 40:1–21

Krasińska M, Krasiński Z (2013) European bison. The Nature Monograph. 2nd Edition, Springer-Verlag, Berlin Heudelberg

Krasińska M, Krasiński ZA, Bunevich AN (2000) Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Białowieża Forest. Acta Theriol 45:321–334

Krishnan L, Guilbert LJ, Russel AS, Wegman TG, Mosmann TR, Belosevic M (1996) Pregnancy impairs resistance of C57BL/6 mice to *Leishmania major* infection and causes decreased antigen-specific IFN-gamma response and increased production of T helper 2 cytokines. J Immunol 156:644–652

Lefèvre T, Lebarbenchon C, Gauthier-Clerc M, Missé D, Poulin R, Thomas F (2009) The ecological significance of manipulative parasites. Trends Ecol Evol 24:41–48

Lloyd S (1983) Effect of pregnancy and lactation upon infection. Vet Immunol Immunopathol 4:153–176

London W, Yorke JA (1973) Recurrent outbreaks of measles, chickenpox and mumps I. Seasonal variation in contact rate. Am J Epidemiol 98: 453–468

Moravec F, Prokopič J, Shlikas AV (1987) The biology of nematodes of the family Capillariidae Neveu-Lemaire, 1936. Folia Parasitol 34:39–56

Moskwa B, Bień J, Cybulska A, Kornacka A, Krzysiak M, Cencek T, Cabaj W (2015) The first identification of a blood-sucking abomasal nematode *Ashworthius sidemi* in cattle (*Bos taurus*) using simple polymerase chain reaction (PCR). Vet Parasitol 211:106–109. doi:10.1016/j.vetpar.2015.04.013

Møller AP (2005) Parasitism and the regulation of host populations. In: Thomas F, Renaud F, Guégan J-F (eds) Parasitism and Ecosystems. Oxford University Press, Oxford, pp 43–53

Møller AP, Erritzøe J, Saino N (2003) Seasonal changes in immune response and parasite impact on hosts. Am Nat 161:657–671. doi:10.1086/367879

Navarro-Gonzalez N, Fernandez-Llario P-MJE, Mentaberre G, Lopez-Martin JM et al (2013) Supplemantal feeding drives endoparasite infection in wild boar in Western Spain. Vet Parasitol 196:114–123

Newton-Fisher NE, Reynolds V, Plumptre AJ (2000) Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest reserve, Uganda. Int J Primatol 21:613–628

O'Connor LJ, Walkden-Brown SW, Kahn LP (2006) Ecology of the free-living stages of major trichostrongylid parasites of sheep. Vet Parasitol 142:1–15

Połeć W, Moskwa B (1994) The development of the early larval stages of *Moniezia expansa* in laboratory conditions. Wiad Parazytol 40:153–157

Pucek Z, Belousova IP, Krasińska M, Krasiński ZA, Olech W (2004) European bison. Status Survey and Conservation Action Plan. IUCN/SSB Bison Specialist Group IUCN, Gland, Switzerland, Cambridge: ix + 54

Pyziel AM, Kowalczyk R, Demiaszkiewicz AW (2011) The annual cycle of shedding *Eimeria* oocysts by European bison (*Bison bonasus*) in the Białowieża Primeval Forest, Poland. J Parasitol 97:737–739

Pyziel AM, Jóźwikowski M, Demiaszkiewicz AW (2014) Coccidia (Apicomplexa: Eimeridae) of the lowland European bison *Bison bonasus bonasus* (L.). Vet Parasitol 202:138–144

Radwan J, Demiaszkiewicz AW, Kowalczyk R, Lachowicz J, Kawałko A, Wójcik JM, Pyziel AM, Babik W (2010) An evaluation of two potential risk factors, MHC diversity and host density, for infection by an invasive nematode *Ashworthius sidemi* in endagered European bison (*Bison bonasus*). Biol Conserv 143:2049–2053

R Development Core Team (2014) R language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria: ISBN 3-900051-07-0, http://www.R-project.org

Raczyński J (2009) European bison Pedigree Book. Białowieża National Park, Białowieża

Raczyński J (2010) European bison Pedigree Book. Białowieża National Park, Białowieża

Raczyński J (2014) European bison Pedigree Book. Białowieża National Park, Białowieża

Regassa F, Sori T, Dhuguma R, Kiros Y (2006) Epidemiology of gastrointestinal parasites of ruminants in western Oromia, Ethiopia. Int Appl Res Vet Med 4:51:57

Shirale SY, Meshram MD, Khillare KP (2008) Prevalence of gastrointestinal parasites in cattle of western Vidarbha region. Vet World 1:45

Shorb DA (1939) Differentiation of eggs of various genera of nematodes parasitic in domestic ruminants in the United States. Technol Bull 694:1–11

Skrjabin KI, Shichobalova NP, Szulc RS (1954) Osnovy nematodologii. Tom III, Trichostrongylidy zhivotnych i čeloveka. Izdatelstvo AN SSSR, Moskva, 1–683

Skrjabin KI, Shichobalova NP, Orlov IV (1957) Osnovy nematodologii. Tom VI, Trichocefalidy i kapilliaridy zhivotnych i čeloveka i vyzyvaemye imi zabolevanija. Izdatelstvo AN SSSR, Moskva, 1–587

Smith KF, Behrens MD, Sax DF (2009) Local scale effects of disease on biodiversity. Ecosyst Health 6:287–295

Stear MJ, Strain SAJ, Bishop SC (1999) Mechanisms underlying resistance to nematode infection. Int J Parasitol 29:51–56

von Szokolay P, Rehbinder C (1984) Deworming of corralled fallow deer (*Dama dama*) using mebendazole. Nord Vet Med 36:394–403 (In Swedish)

Taylor MA, Coop RL, Wall RL (2007) Veterinary Parasitology, 3rd edn. Blackwell Publishing, Oxford, UK

Thomas F, Poulin R, de Meeûs T, Guégan J-F, Renaud F (1999) Parasites and ecosystem engineering: what roles could they play? Oikos 84: 167–171

Thomas F, Bonsall MB, Dobson AP (2005) Parasitism, biodiversity, and conservation. In: Thomas F, Renaud F, Guégan J-F (eds) Parasitism and Ecosystems. Oxford University Press, Oxford, pp 124–139

Thompson RCA, Lymbery AJ, Smith A (2010) Parasites, emerging disease and wildlife conservation. Int J Parasitol 40:1163–1170. doi:10.1016/j.ijpara.2010.04.009

Tokarska M, Pertoldi C, Kowalczyk R, Perzanowski K (2011) Genetic status of the European bison *Bison bonasus* after extinction in the wild and subsequent recovery. Mammal Rev 41:151–162

Treboganova N (2010) Behavior of the bison and helminthoses. Eur Bison Conserv Newsl 3:125–134

Tylkowski J (2013) Characteristics of annual air temperature, thermal seasons and the vegetation seasons in Dziwnów. Monitoring Środowiska Przyrodniczego 14:127–134 (In Polish)

Wakelin D (1985) Genetic control of immunity to helminth infections. Parasitol Today 1:17–23

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effets models and extensions in ecology with R. Springer, New York